Foraging Responses of *Veromessor pergandei* to Changes in Seed Production

(Hymenoptera: Formicidae)

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The desert harvester ant, *Veromessor pergandei* (Mayr), is a major component of the ecosystem in the Mohave Desert. In Death Valley National Monument, nests can be very extensive and long-lived, even though this is the northern limit of its range (Wheeler and Rissing in press). In Death Valley *V. pergandei* has a biomass per unit area approximately equal to that of the total rodent population in the same area (Went *et al.* 1972). Colonies of this species survived in the Coachella Valley of California even after twelve successive years of severe drought (Tevis 1958).

The abundance of this species and its ability to withstand long periods of drought and the consequent scarcity of food must be the result of an efficient food gathering strategy developed for the desert environment. We have observed this strategy following a profuse bloom of winter annuals in 1973 and a significantly less abundant bloom in 1974.

During the early summer *V. pergandei* has two foraging periods. One starts in the early morning often before there is any indication of sunlight in the sky to the human observer; this period ends when the temperature becomes too high (apparently). The second period starts in the afternoon after the temperature has fallen from the noon high and may continue after dark on warm evenings. By consecutive foraging periods we are referring to any combination of possible time-adjacent foraging periods. However, we omitted numbering the periods when no foraging activity was observed. At Nest 1 this occurred 7 out of 13 and at Nest 2, 4 out of 13 possible evening foraging periods. Foraging columns were observed at Nests 1, 2 and 4 during all possible morning foraging periods.

Materials and Methods: Observations were made on selected nests at a site in the north end of Death Valley National Monument near Grapevine Ranger Station at 800 m elevation (see Wheeler and Rissing

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in press for full description). The nest numbers and locations are the same as those described previously; since 1973 Nests 5 and 8 have been disturbed by road construction, Nest 10 has become inactive, and Nest 4 (15 m east of Nest 2) has been added to the list of nests studied.

Several properly timed rains which produced abundant germination of winter annuals preceded the 1973 study period. Later adequate rains favored plant growth and a profuse setting of seed during the spring and summer of 1973. In comparison, the rains preceding the spring and summer of 1974 were less and resulted in poorer germination, plant growth, and seed production for most plants. For this study, all evaluations of germination and seed production were very kindly provided by Dr. F. W. Went from his long-term observations at this and other sites in Death Valley (personal communication).

Regular observations were made from 19 May to 21 June 1973, and from 10 June to 23 June 1974. In 1973, the directions of the foraging columns at four nests were recorded. Periodic samples of the items foraged at eight nests in the study area were taken by aspirating returning foragers from a smooth surface near the nest entrance at the height of foraging activity. The items were later separated from the ants and identified under a stereomicroscope. In 1974, the column direction and a sample of items foraged were taken each foraging period at Nests 1 and 2. Observations were begun on the column direction at Nest 4 on 15 June 1974.

Results: Column descriptions and results of samples of items foraged for the 1973 portion of this study are reported elsewhere (Wheeler and Rissing in press). Figures 3, 4, and 5 show the direction of foraging columns at Nests 4, 1, and 2 in 1974. The numbers and percentages of each foraged item are shown in Table 1, which also includes the cumulative data from the 8 nests observed in 1973.

Discussion: 1. Direction Change And Foraging Method: Studies have been conducted concerning the foraging pattern of *V. pergandei* (Bernstein fide Carroll and Janzen 1973; Went *et al.* 1972; Wheeler and Rissing in press). Went *et al.* reported that foraging column direction changed 15° between consecutive foraging periods. Bernstein reported a change of approximately 20°, but only when seeds were scarce; when seeds were abundant she reported random foraging was preferred to column foraging.

Fig. 1 and 2 show the frequency of degrees of change in column direction between successive foraging periods in 1973 and 1974 respectively. The data from both years fail to support the observation that there is some constant by which column direction changes between

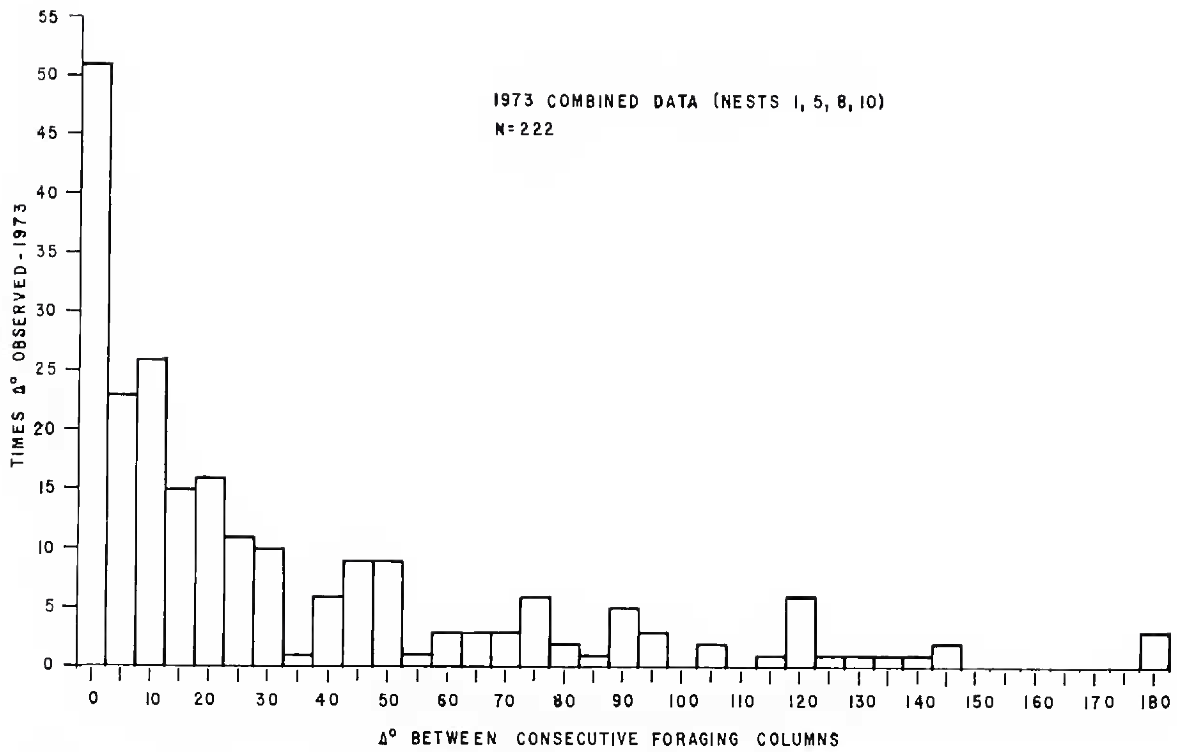

FIG. 1. Histogram showing the frequency of degrees changed between consecutive foraging columns, 1973 data.

successive foraging periods. It appears, however, that in 1973 there was usually little if any change in column direction between successive foraging periods and that when this direction did change the amount was usually small. In 1974 column direction changed more often, and the amount of change between successive periods was quite variable. The difference between the two years may be in response to the difference in seed production in 1973 and 1974. In 1973 seeds were very abundant and probably uniformly scattered over the foraging area. In 1974 it may have become necessary to explore all available areas for local and temporary concentrations of seeds.

In 1973, when seed production was enormous, random foraging was rarely observed; almost always columns were long and populous. In 1974, when seed production was much less, the column was still the

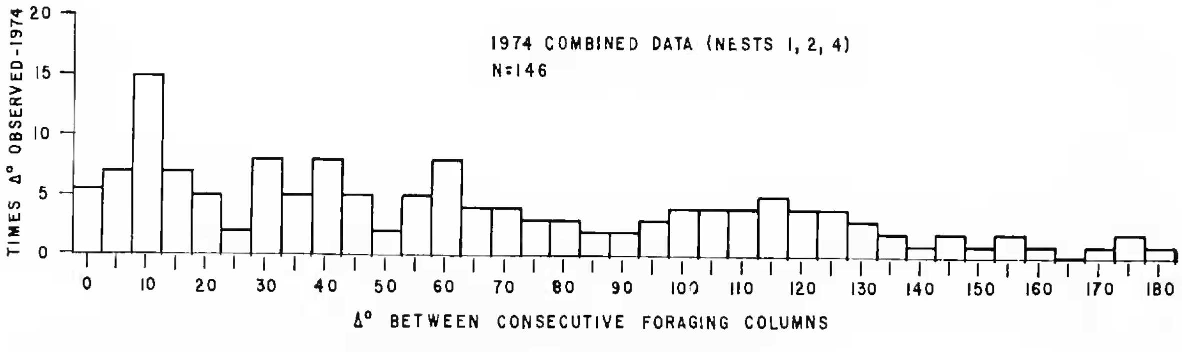

FIG. 2. Histogram for 1974 columns. (See Fig. 1.)

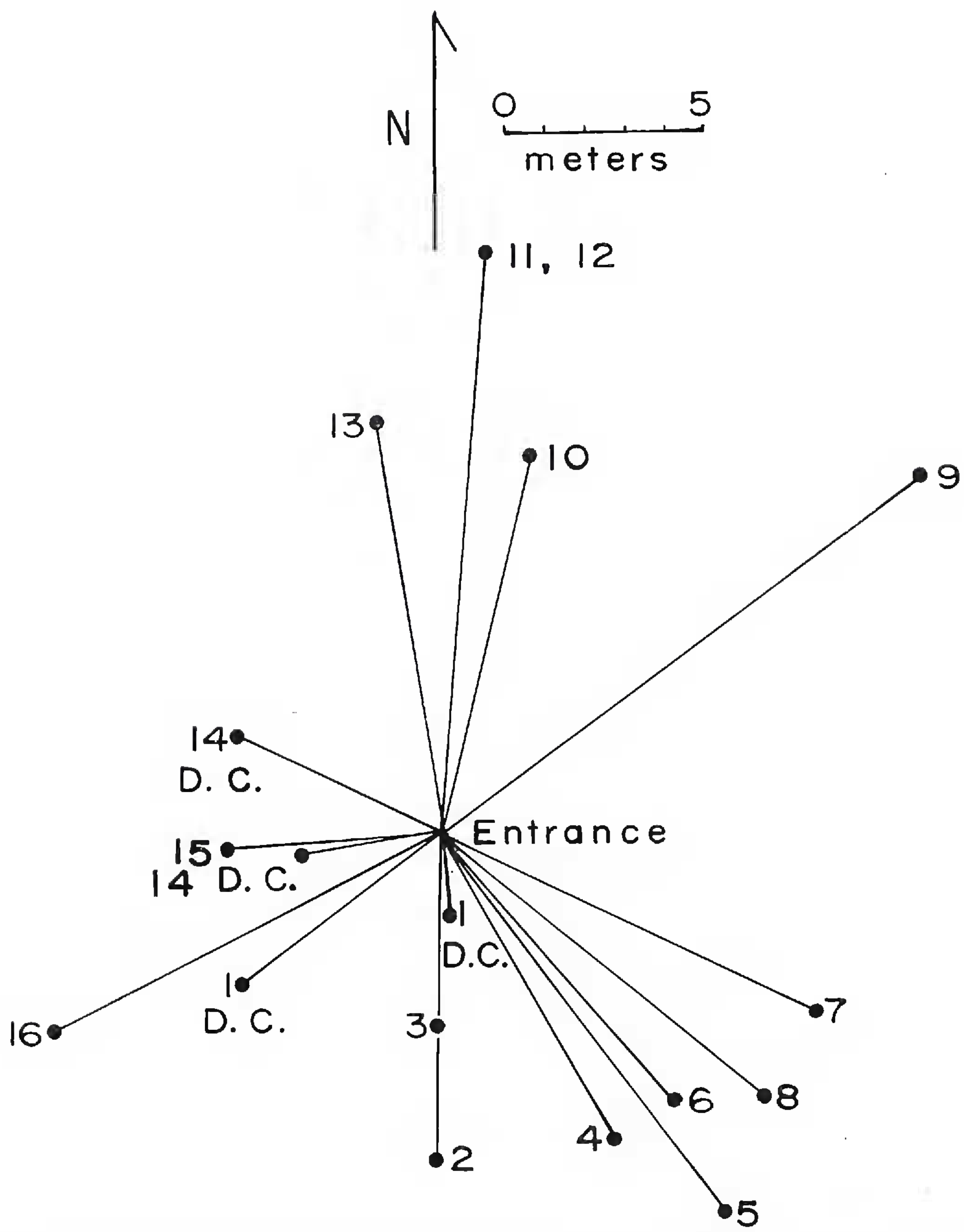

FIG. 3. Observed directions (clockwise from north) and lengths of foraging columns during consecutive foraging periods at Nest 4. D. C.: double column.

most common foraging pattern; however, infrequent periods of random foraging were noted, especially at Nest 1. This does not agree with Bernstein's report of column foraging only when seeds were more abundant. It is also interesting that Tevis (1958) noted no shift to random foraging in 1957, when seed production was high for the first time in twelve years.

While the amount of change between consecutive foraging periods was variable in 1974, succeeding columns generally rotated about each individual nest in a characteristic clockwise or counterclockwise fashion. The simplest case during this study was Nest 4 (Fig. 3) where successive columns rotated in a counterclockwise fashion. This, how-

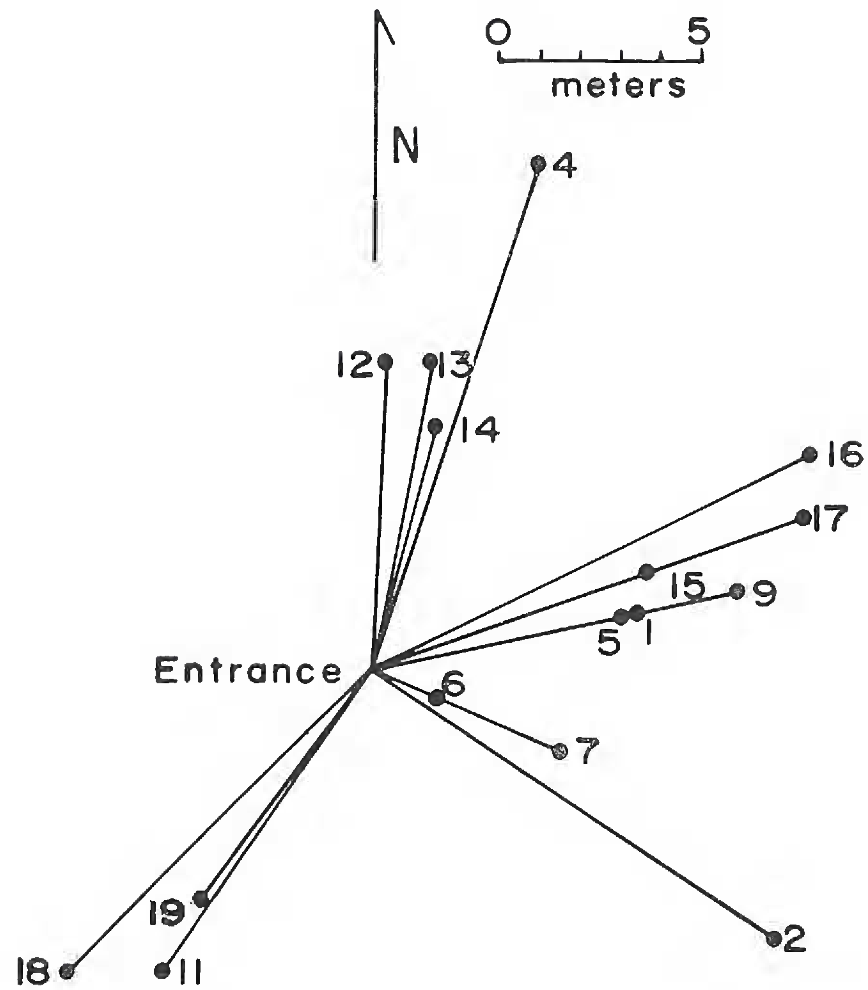

FIG. 4. Observed columns at Nest 1. For explanations see Fig. 3. During foraging periods 3, 8, and 10 no columns were formed and random foragers were seen.

ever, was achieved in uneven steps and included some clockwise "backstepping" (e.g., foraging periods 8 and 15).

The direction change of the columns at Nest 1 (Fig. 4) was more complicated, but seemed to occur in a general clockwise rotating pattern. During periods 3, 8, and 10, the typical long, straight column of foragers was not seen; instead individual foragers left the nest in random directions (= random foraging). Columns from this nest generally did not forage in the area to the west and northwest of the nest entrance because there were no plants under the Desert Research Institute's mobile laboratory nor in the gravel road. The columns "swept" the available area from 0° to 220°; one such sweep was completed during foraging periods 12 through 19. As was true at Nest 4, some changes did occur in the direction opposite to that typical for this nest (i.e., periods 16 and 19).

The columns at Nest 2 (Fig. 5) swept an even smaller area. This avoided foraging (1) in the adjacent gravel road (which runs past

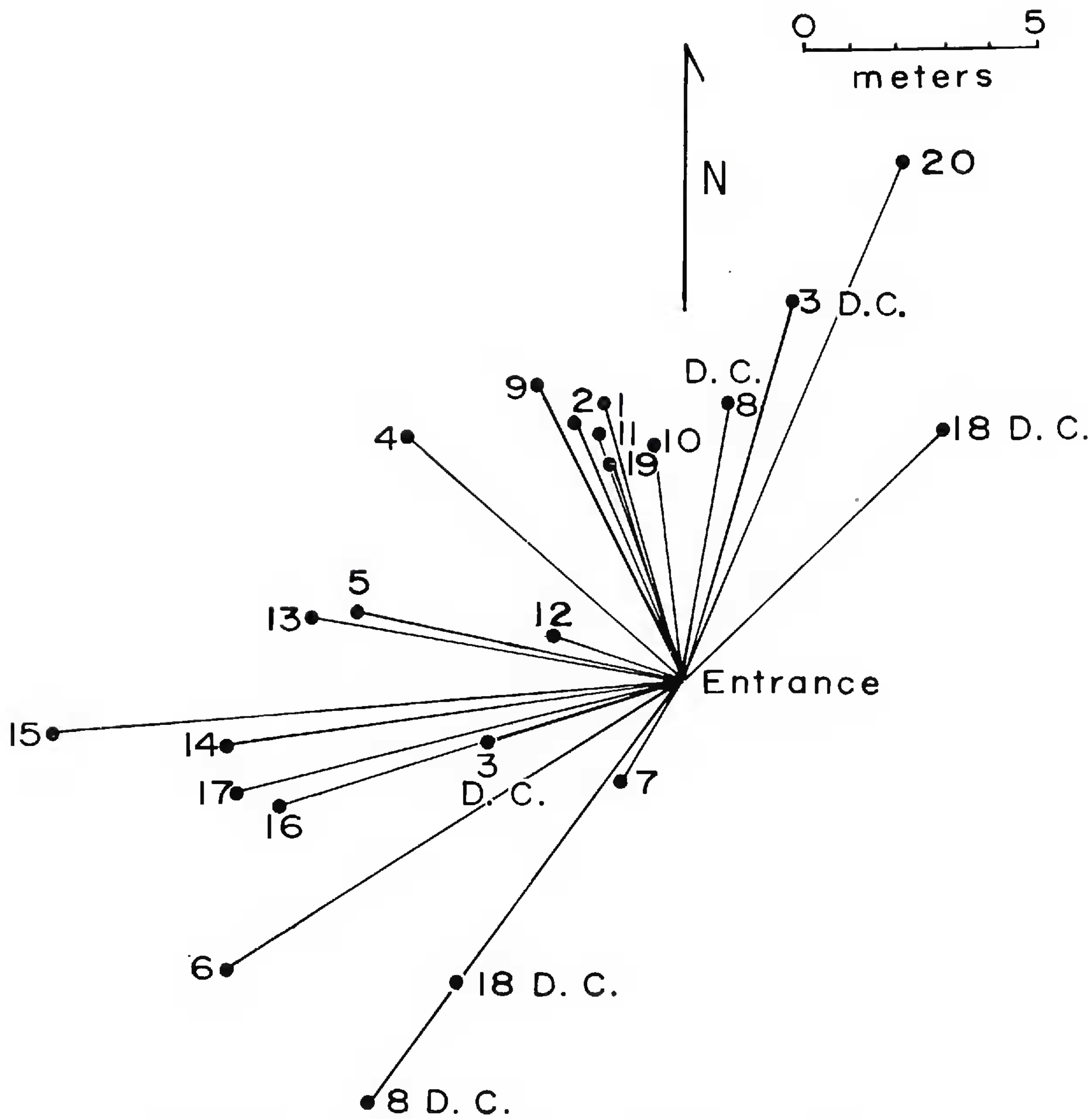

FIG. 5. Observed columns at Nest 2. For explanation see Fig. 3.

this nest from southwest to northeast), and (2) in the foraging area of Nest 4 (15 m to the east), and (3) in the foraging area of Nest 1 (12 m to the south). Two full counterclockwise sweeps of the area about Nest 2 are shown in Fig. 5, along with the start of a third. At this nest clockwise "backstepping" occurred during periods 10, 15, 17 and 20 and for one of the double columns which occurred during periods 3 and 8. It is very interesting that during periods 8 and 18 double columns were seen: one column at 218° and the other at 10° (period 8) and 218° and 45° (period 18). These particular columns seemed to mark the end of one sweep and the start of the next.

2. Response To Diminished Annual Seed Production: *Veromessor pergandei* responded to the lower seed production by winter annuals in three ways: (a) increased collection of non-seed plant material, (b)

decreased collection of seeds which had become scarce, and (c) increased collection of "less desirable" seeds. (See Table 1.)

(a) Non-seed Plant Material: In 1973, 12.6% of all items collected was non-seed plant parts; this increased to 27.2% following the lower seed production of 1974. In both seasons most of this material was flower parts of *Lygodesmia spinosa* Nutt., smaller amounts of unidentifiable flowers, leaves, and stems were also found. The exact use of this and other non-seed material (arthropod exoskeletons and fecal material) is unknown, but they were rarely found in the refuse pile. The suggestion by Went *et al.* (1972) that these materials might be used in some sort of fungus garden is a possibility.

(b) Scarce Seeds: The general decrease in seed production between 1973 and 1974 is reflected by the fact that 85.4% of all items collected by the foragers in 1973 were seeds; in 1974 only 71.5% were seeds. In April 1972, Clark and Comanor (1973) observed that 88% of 252 foraged items were seed and fruits. Tevis (1958) observed, during a period of drought and poor seed production, that 68.2% of all items collected by this same species were seeds. This increased to 91.9% following timely winter rains and a productive spring.

Among the different species of seeds there were notable differences between 1973 and 1974. Fewer plants of *Mentzelia albicaulis* Dougl. ex Hook. grew in the study area in 1974, and the seeds of this species were collected one tenth as often. *Mohavea breviflora* Cov. and *Oenothera clavaeformis* Torr. & Frém. had fewer and smaller plants in 1974, and the percentages of seeds of both of these species decreased. Some plants, like *Phacelia calthifolia* Brand and *Ph. crenulata* Torr., simply did not germinate in 1974. Differences like that for *Chaenactis stevioides* H. & A. between 1973 and 1974 may be a result of fewer nests observed in the latter year. This composite was found only near Nest 3 which was not observed in 1974.

A notable exception to decreased collection of annual seeds occurred with *Cryptantha angustifolia* (Torr.) Greene which represented 9.7% of all items collected in 1973 and 20.7% in 1974. While the plants of this species were much smaller in 1974, they were still numerous and produced large numbers of seeds.

In 1973 the seeds of 29 species of plants representing 24 genera were collected by the foragers. This compares with seeds from 20 species in 16 genera in 1974. Clark and Comanor (1973) reported that seeds from four species of plants (representing 4 genera) were collected by this species at our study site in April 1972. Meaningful comparisons with this study are unfortunately precluded by its brief duration (4

Table 1. Samples of items (number and percent) from foraging columns at Nests 1 and 2 in 1974 and from all nests in 1973.

Seeds of Species	Nest 1, 1974		Nest 2, 1974		Total 1974		Total 1973	
	Number	%	Number	%	Number	%	Number	%
Malvastrum rotundifolium			1	0.1	1	0.1	2	0.1
Larrea divaricata	3	0.3	5	0.2	8	0.3		
Mentzelia albicaulis	3	0.3	10	0.5	13	0.4	114	3.9
Lepidium lasiocarpum							7	0.2
Chorizanthe brevicornu	10	1.1	87	4.0	97	3.1	26	0.9
Chorizanthe rigida			4	0.2	4	0.1		
Eriogonum inflatum	97	10.3	240	11.0	337	10.8	83	2.8
Eriogonum pusillum	6	0.6	87	4.0	93	3.0	47	1.6
Chenopodium pumilio	149	15.8	137	6.3	286	9.1	252	8.5
Atriplex hymenelytra	13	1.4	5	0.2	18	0.6	55	1.9
Plantago insularis fastigiata			3	0.1	3	0.1		
Gilia filiformis	2	0.2	2	0.1	4	0.1	6	0.2
Gilia latifolia	1	0.1			1	0.1	26	0.9
Gilia sp.			3	0.1	3	0.1		
Phacelia calthifolia							7	0.2
Phacelia crenulata							25	0.9
Cryptantha angustifolia	203	21.5	447	20.4	650	20.7	285	9.7
Cryptantha holoptera							76	2.6
Cryptantha nevadensis	2	0.2	2	0.1	4	0.1	18	0.6
Nicotiana trigonophylla							2	0.1
Mohavea breviflora							68	2.3
Dalea sp.			8	0.4	8	0.3		
Oenothera clavaeformis	177	18.7	129	5.9	306	9.8	951	32.2
Nemacladus glanduliferus							1	0.1
Bebbia juncea							8	0.3
Hymenoclea salsola	2	0.2	2	0.1	4	0.1	4	0.1
Franseria dumosa	17	1.8	69	3.2	86	2.7	53	1.8
Chaenactis stevioides	2	0.2	2	0.1	4	0.1	151	5.1
Monoptilon bellioides							4	0.1
Psathyrotes ramosissima			1	0.1	1	0.1		

Table 1 (cont.)

Seeds of Species	Nest 1, 1974 Number	%	Nest 2, 1974 Number	%	Total 1974 Number	%	Total 1973 Number	%
Peucephyllum schottii			1	0.1	1	0.1	19	0.6
Lygodesmia spinosa	40	4.2	251	11.5	291	9.3	192	6.5
Calycoseris parryi							4	0.1
Atrichoseris platyphylla							9	0.3
Unknown Seeds	3	0.3	7	0.3	10	0.3	30	1.0
TOTAL SEEDS	730	77.2	1503	69.0	2233	71.5	2525	85.4
Non-seed Plant Parts	195	20.6	609	27.8	804	25.7	372	12.6
Arthropod Parts	8	0.9	40	1.8	48	1.5	38	1.3
Lizard and Rodent Droppings	9	1.0	34	1.6	43	1.4	16	0.6
Gravel							3	0.1
TOTAL NON-SEED	212	22.5	683	31.2	895	28.6	429	14.6
TOTAL NUMBER OF ITEMS	945		2186		3128		2954	
NUMBER OF SAMPLES	16		25		41		69	

days), number of nests observed (one), low number of items identified as they were carried past the observer (N = 252), and what seems to be aberrant behavior of the single nest watched. The largest number of foragers reported in a column never exceeded 250—an unusually low number compared to our experience at this site. Tevis (1958) reported seeds from 14 genera of plants for his entire study. By comparison, Rogers (1974) found that the harvester *Pogonomyrmex occidentalis* (Cresson) collected seeds from 39 species of plants representing 32 genera at the IBP Grassland Biome, Pawnee Site, in northeastern Colorado. Wheeler and Wheeler (1963) reported seeds of 30 species in 26 genera collected by *P. occidentalis* in North Dakota.

(c) "Less Desirable" Seeds: *Chorizanthe brevicornu* Torr., an annual with a hard, thick seedcoat, germinated and set seed equally well in 1973 and 1974, yet it was collected more often in 1974. A closely related species *Chorizanthe rigida* (Torr.) T. & G. was abundant both years but the refuse piles of nests (other than those studied intensively) in the study area contained large amounts of this seed in 1974, whereas none were found in any refuse piles in 1973. Most of these seeds had been opened by the ants. Seeds from perennials, such as *Franseria dumosa* Gray and *Lygodesmia spinosa*, were equally abundant in both years yet both were collected more often in 1974. While these seeds increased in relative abundance, they may have been ignored originally due to excess energy required to extract the seed from a hard and difficult-to-open seed coat. They were collected only when other seeds were less plentiful.

Conclusions: We have stated previously (in press) that *V. pergandei* is very plastic in its behavior: e.g., in nest construction and interchangeability of worker roles. This plasticity is seen again in the ability of this species to make changes in its foraging in response to the varying productivity in the desert plant community. Indeed, this behaviorial plasticity must be a major reason why this species is one of the most abundant animals in the Mohave Desert even during extreme drought. Certainly such behavior is a beautiful example of adaption for the extremely varied conditions of the Mohave Desert and contributes to the predominance of *V. pergandei* in that environment.

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